

Original papers

Water relations of coastal plant communities near the ocean/freshwater boundary

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Summary. Salinity and isotope ratios were determined in water from several wells in the Florida Keys, and tidal inlets. Both D/H and $^{18}\text{O}/^{16}\text{O}$ ratios of water from wells and tidal inlets were highly correlated to their salinity. Water from standing pools was enriched in deuterium and oxygen-18 relative to their salinity because of evaporation processes. $^{18}\text{O}/^{16}\text{O}$ and D/H ratios of stem water from plants of several different communities at Sugar Loaf Key, ranging from hardwood hammocks to mangroves, were highly correlated to their predawn water potential. The correlation was consistent with the presence of high salinity in waters with high ^{18}O and D content. Most individuals from each community were either utilizing water with isotopic characteristics typical of freshwater or of ocean water, while only a few individuals had stem water with isotopic ratios intermediate to these two water sources.

Key words: Water potential – Mangrove – Hardwood hammock – Salinity – Stable isotopes

South Florida and many other areas in the Caribbean basin have a flat topography which allows for the interaction between saline ocean water and rain-derived freshwater. This interaction has produced a mosaic of several vegetation types exhibiting different salinity tolerances, ranging from saline tolerant mangrove vegetation to relatively non-tolerant hardwood hammock and cypress stands (Hoffmeister 1974). Previous research has shown that freshwater and ocean water in South Florida have different isotopic compositions, with freshwater showing less deuterium and oxygen-18 enrichment than ocean water (Sternberg and Swart 1987). It was also shown that by analyzing plant water, many interesting questions regarding the placement of various coastal communities in the interface between freshwater and ocean water can be answered. Three major communities were analyzed;

hardwood hammock, mangrove margin, and mangrove. The mangrove margin community was loosely identified as a community occurring in sandy berms in the midst of mangrove. Plants in this community were characterized by succulent stem or leaves, with such species as *Borreria frutescens* L.(DC.) and *Sesuvium portulacastrum* (L.)L. The findings of this previous study showed that hardwood hammocks were located in the freshwater end of the salinity spectrum, mangrove margin species occupied the middle of the spectrum, and mangroves, although mostly in the ocean water end of the spectrum, had several individuals utilizing freshwater. Implicit in these conclusions is the assumption that salinity and isotopic ratios follow a linear relation caused by the various proportions of freshwater and ocean water during mixing. There are at least two ways in which this relationship does not hold. Firstly, rain water can mix with salts deposited by high tides, thus giving that water elevated salinities but isotopic ratios typical of freshwater. Secondly, freshwater bodies can undergo evaporation causing isotopic enrichment thus giving them high isotopic ratios typical of ocean water but low salinities typical of freshwater. In order to detect deviations from a simple ocean-freshwater mixing model we determined the isotopic composition and salinity from water of 28 wells through out the Florida Keys (Fig. 1). Salinity of water from these wells ranged from 2‰ to 40‰. In addition we sampled water from several bays and tidal flows through out the Florida Keys (Fig. 1).

We further hypothesized that if the salinity of water is related to its isotopic composition, plant predawn water potential should be related to the isotopic composition of stem water. This relationship may be possible in southern Florida because its high rainfall minimizes the effect of soil matric potential as a determinant of plant predawn water potential. Plant predawn water potential should, therefore be mostly related to the soil water osmotic potential. Thus to determine whether the overall water status of different plant communities is dependent on where they are placed along a gradient of

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The Florida Keys, having a latitude of approximately 24 degrees, were considered subtropical. Annual rainfall over the period 1951-1980 averaged 1052 mm; mean yearly temperature was 25.3°C. There is a marked seasonality in precipitation with a dry season from November to April and a wet season from May to October. Approximately two-thirds of the rainfall falls during the wet season. Major storms and hurricanes occur most frequently from June to October. Rainfall during the study period was below normal although the rainfall over the previous year was above normal. The mean temperature was 25.1°C and the mean humidity was 70.7% over the period from March to August. No major storms or hurricanes occurred during this period.

Climatic

The coarse communities sampled were mostly hammocks (site HH; high salinity) and HL; low salinity), transitionally oolithic woodland (site W), rocky scrub mangrove dominated by *Coccoloba uvifera* (site L), and RSM (site RSM) and a taller scrub mangrove community (site ER). Hammocks key are a diverse assemblage of *Acacia farnesiana* (Baker), *Pisidium longipes* (Berg), and many others. These forests are of relatively modest stature, with the two stands at higher elevations (Baker), *Pisidium longipes* (Berg), and many others. Hammocks have in a canopy of between 4 m to 7 m. The soils in these sites were organic and shallow. Ground water ranged from 0.4 to 0.7 m below the surface of the two hammocks sampled. Site HH had a mean ground water salinity of 14.7% over the October 1989 - December 1990 period and site HL had a mean ground water salinity of 14.7% over the October 1989 - December 1990 period. Neverthelesss the sites were of similar species composition and structure. Transitionally woodland areas are typical of 3-4% over this same period. Nevertheless the sites were of similar soil less than 2 cm deep. This area had pockets of shallow organic soil less than 2 m), scattered clumps of *C. erectus*, *Laguncularia racemosa* (L.), *Garcinia* L., *Rhizophora mangle* L., and *Aracena* L. (L.). Also present are a few species of succulent herbs and some grasses. Soil is heterogeneous usually deeper and more continuous than site RSM. Ground water was a mean of 0.06 m below ground and had a mean salinity of 35‰.

Stem water and water potentials were sampled from 5 com-munities on Sugarloaf Key on March 29, June 27, and August 8, 1990 (Fig. 1). Plants were identified using Long and Lakela (1978). The surface geology of Sugarloaf Key consists of an oolithic facies known as Miami oolite, with a surface layer of calcarenous marine sediments (Devere et al. 1986). The cap is more dense and less permeable than the underlying Miami oolite. Soils on the key are Haplorthemic, marl, peat, coarse sand, or some combination of these four soil types. The soils are generally thin and heterogeneous due to the topography of the island. Most of the island is above sea level, but there is a maximum elevation of 1.5 m above sea level.

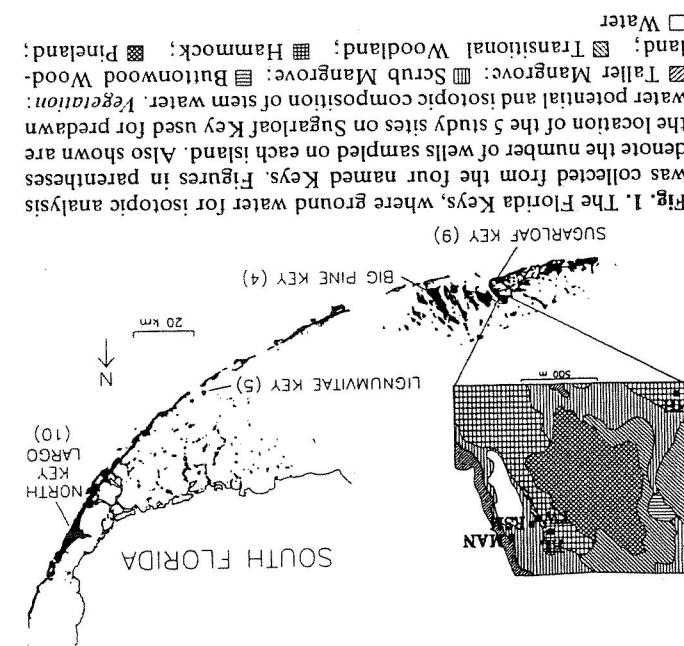
Soil was collected at a high salinity hammock (site HH) at the approachable depth of 15 to 20 cm. Soil was sealed in a ring seal vessel and taken to the lab for distillation. The amount of water distilled from the soil was measured volumetrically, and stored for isotopic analysis. Dry soil was weighed, and the percentage of water moisture was calculated using the volume measurement of water extracted by filtration and used for salinity measurements. Using known volume of distilled water, Water from this mixture was known weight. Dry soil was then mixed for 1 hour with a known volume of distilled water. Water from this mixture was then weighed, and the difference between the two weights was the amount of water extracted by filtration.

Analysis of soil water

Ground water samples from the Keys were collected from 28.5 cm diameter wells. The distribution of these wells is shown in Fig. 1. 22 wells were drilled in the spring of 1989 with the assistance of the U.S. Geological Survey. These wells were drilled to a depth of at least 1.5 m below sea level. 6 additional wells were drilled in the fall of 1989 to a depth of 0.3 m below sea level. All were constructed with well screening and a section of solid casing was sealed to the bedrock to prevent infiltration of surface water. Salinity of the wells was monitored biweekly during this study (March to August 1990) with a salinity-conductivity temperature meter (YSI, model 33). Measurements were taken at 1.6 m intervals until the bottom of the well was reached. Water samples were collected in bottles and tightly sealed in a container for isotopic analysis in November of 1989 and January 1990 at the surface of the ground-water table and in January 1990 at the surface of the ground-water table.

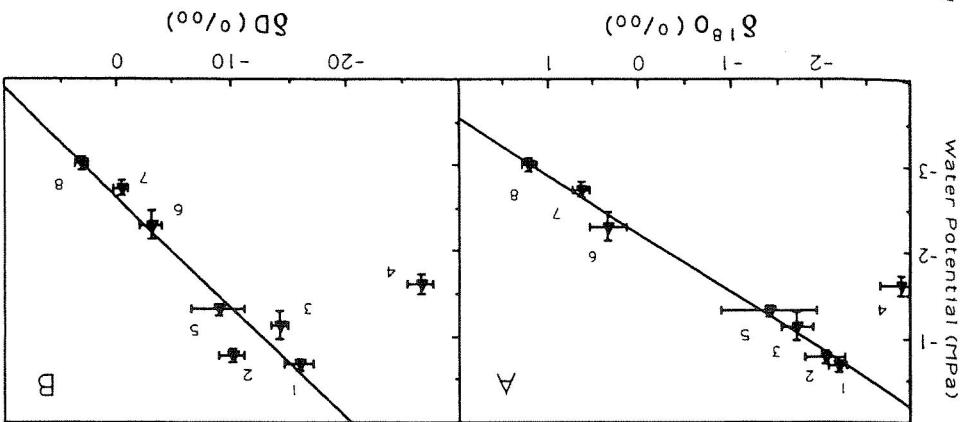
Analyses of groundwater

ocean water and freshwater mixtures, we measured the isostopic composition of stem water and predrawn water potential for different plant communities at various locations relative to ocean water, ranging from mangroves, the closest to ocean water, to hammocks, (the furthest from ocean water).



samplesd on June 27. Number by each point represents the following sites sampled at a given date as described in the materials and methods: 1 - HL, March 29; 2 - HL, August 8; 3 - HH, March 29; 4 - TW, June 27; 5 - TW, August 8; 6 - RMs, August 8; 7 - MAN, March 29; 8 - MAN, August 8

$P = 0.91$, $\delta^{18}\text{O} = -2.21 - 0.68 (\delta^{18}\text{O})$, $r^2 = 0.99$). Regression values of plant stem water potential for each community versus average predrawn water potential for each site (δD) = $-2.62 - 0.13 (\delta\text{D})$. δD does not include average values for transition woodland sites sampled on June 27. Values of plant stem average $\delta^{18}\text{O}$ (A) and δD (B)



$\delta^{18}\text{O}$ values fall close to values observed for source water, here. (*Fig. 3*).

lowest δD and $\delta^{18}\text{O}$ values for all communities sampled than hammock species, yet had stem water with the lowest δD hammock had plants with lower predrawn water potential than woodland sampled in June, 1990 at the border of a hammock usage of saline ocean water. The transition area stem water, the lower the higher the δD and $\delta^{18}\text{O}$ values of plant in general the higher the ratio of stem water (*Fig. 3*). Thus, related with isotopic ratio of stem water was highly correlated 1990, predrawn water potential was sampled in one plant community (transition woodland) between different communities (Table 1). With exception of June 1990, predrawn water potential of plant sampled in November not associated with surface waters, and $\delta^{18}\text{O} = -13.149 + 0.1613 * \text{Sal} + 0.023676 * \text{Sal}^2$, $r^2 = 0.88$, $P < 0.01$; $\delta\text{D} = -13.149 + 0.1613 * \text{Sal} + 0.012577 * \text{Sal}^2$, $r^2 = 0.938$, $P < 0.01$. Symbols: □ for wells not associated with surface waters, ■ a well in a seepage zone water pool, ● soil water, and ▲ for water samples from Florida Bay (*Swart et al. 1989*).

Although there were some variability in water potential, this variation, in most cases, was less than that between different communities (*Table 1*). Salinity of soil water was on the average $6.1 \pm 3.6\%$ ($\pm \text{SE}$), and constituted approximately 45% of soil content. Salinity of soil water was on the average $6.1 \pm 3.6\%$ ($\pm \text{SE}$), and constituted approximately 45% undergoing evaporation (*Fig. 2*). The relationship between δD and $\delta^{18}\text{O}$ values of water was highly significant ($P < 0.01$). Soil water showing a slope of 5.1 ($r^2 = 0.92$, $P < 0.01$). Soil water had lower δD values but similar $\delta^{18}\text{O}$ values as fresh water except for wells located in standing pools of water (*Fig. 2*). The relationship between soil salinity and $\delta^{18}\text{O}$ values was highly correlated ($P < 0.01$).

Results

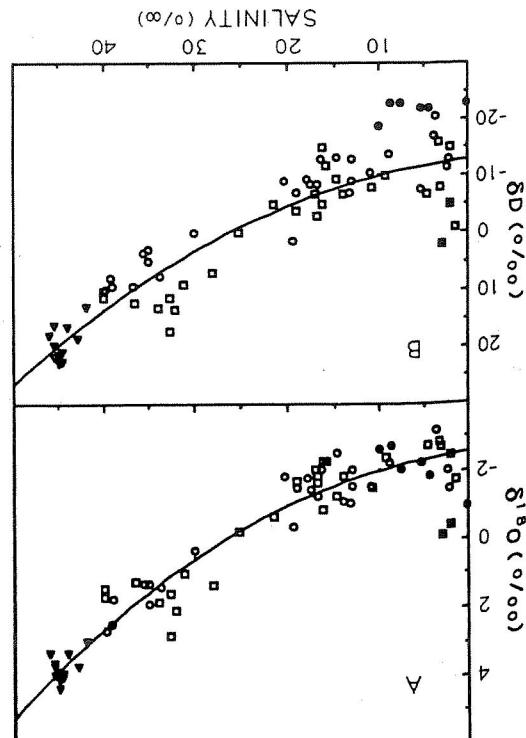
where R is the $\text{O}_{18}/\text{O}_{16}$ and D/H ratios of sample and standard (SMOW). δ values are reported here relative to Standard Mean Ocean Water (δSMOW).

Oxygen isotope ratios were determined by equilibrium with carbon dioxide as described by Epstein and Mayeda (1953). All isotopic ratios are reported in δ units where $\delta\text{‰} = [(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1]1000$.

Hydrogen isotope ratios were determined by passing 2 to 4 μl of water through a hot uranium furnace (750°C) as described by Blaglesien et al. (1952). Hydrogen released from this reaction was collected with a Toepler pump and used for isotopic analysis.

Isotopic analysis

Fig. 2A, B. $\delta^{18}\text{O}$ (A) and δD (B) values of well and soil water versus salinity. Regression for well waters only: $\delta^{18}\text{O} = -2.5911 + 0.023676 * \text{Sal} + 0.0025853 * \text{Sal}^2$, $r^2 = 0.883$, $P < 0.01$; $\delta\text{D} = -13.149 + 0.1613 * \text{Sal} + 0.012577 * \text{Sal}^2$, $r^2 = 0.938$, $P < 0.01$. Symbols: □ for wells not associated with surface waters, ■ a well in a seepage zone water pool, ● soil water, and ▲ for water samples from Florida Bay (*Swart et al. 1989*).



Predrawn water potential of plants in the transitional woodland community sampled in June, 1990 were significantly lower than hammock species, yet their stem water samples had the lowest δD and $\delta^{18}O$ values for all communities sampled here. (Fig. 3). The low δD and $\delta^{18}O$ values of stem water is a clear indication of rainwater usage by this community. These species may be located in a region unusually high tides or salt spray, thus accounting for its mixiture of rainwater and salts deposited by the wind. A mixture of rainwater and salts deposited by the wind is similar to freshwater species. Alternately, plants in this community may have low water potentials for lack of water, since June 1990 measurements in this community were done at the end of the dry season, and this community lacks soil as found in the hardwood hammocks. We do not have sufficient data to determine the cause of the unusually low δD and $\delta^{18}O$ values of stem water in this community. We do have sufficient data to determine the cause of the unusually low δD and $\delta^{18}O$ values of stem water in this community. There could be at least two reasons for these isotopic ratios. Firstly,

The relationship between average plant predrawn water potential for each community and isotope ratios of their stem water (Fig. 3) is predicted on the basis of the following reasoning. Deutrium and oxygen-18 content of subsurface water is indicative of salinity (Fig. 2), and plant predrawn water potential is highly related to the salinity of the water the plant is using (Scholander 1965). Thus predrawn water potential is inversely related to the face water should be related to the isotope ratios of the face water in their stem. Plants from a hardwood hammock with a shallow water table, having a salinity of averaging 14.7%, showed less than expected differences in predrawn water potential relative to a hammock having a water table with a salinity averaging 3.4% (Table 1). We expect the predrawn water potential of this community to be about -2.0 MPa; in between water potentials of the freshwater hardwood hammock (-0.68) and mangroves (-3.02), and yet the average predrawn water potential value for plants in this community was -1.14 ± 0.16 (Table 1). We hypothesize that the hammock exposed to a high salinity water table may be using water stored in the soil layer with lower salinity. Thus soil water may buffer the effects of high salinity in the water table of a high salinity water table (Table 1).

Soil water from the HH site constituted about 45% (w/w) of soil with a salinity averaging only $6.1 \pm 3.6\%$ even though the water table in this site had a salinity averaging 14.7%. δD and $\delta^{18}\text{O}$ value of soil water were similar to wells having water with low salinities (Fig. 2). There is no trend in δD values of soil water relative to salinity, but an apparent decrease in $\delta^{18}\text{O}$ values with increasing salinity. Further sampling will be necessary to determine whether this relationship holds. δD versus $\delta^{18}\text{O}$ value of soil water fall in line with a slope close to 0.0 indicating a proportionally greater enrichment in oxygen-18 than deuterium. The reason for this slope has been previously ascribed to kinetic fractionation effects during diffusion through the soil boundary (Fig. 3).

salinities but isotopic ratios similar to freshwater have been previously observed in Cluett Key (Swart et al.

Only small differences were observed in isotopic ratios for water having salinities between 2 and 20‰. Followed by a gap of water samples having salinities between 20 and 30‰, and their corresponding isotopic compositions (Fig. 2). The gap in intermediate values of salinity and isotopic ratios may be caused by a sharp interface between ocean and freshwater. Thus the probability of a well being in a mixing zone is low. Wells sampled here were chosen so as to represent a transect from freshwater tables to ocean water, and yet relatively few wells had values to ocean water with intermediate values between 5‰ and +5‰ and -1‰ and +1‰. For δD and $\delta^{18}O$ water with intermediate δD and $\delta^{18}O$ values between -5‰ and +5‰ and -1‰ and +1‰ and water having salinity mixtures with rainwater. Soil water having high salt spray deposit salts, leaving a "salt front" which because in certain areas unusually high ocean tides, or may vary their salinities from 2‰ up to 20‰, probably respectively. Water from wells with lower isotopic ratios especially.

δD and $\delta^{18}\text{O}$ values of well water are correlated with salinity (Fig. 2). This correlation is in part due to the mixing of freshwater and ocean water having different salinities and isotopic compositions. δD and $\delta^{18}\text{O}$ values of water from an area in Big Pine Key (Fig. 2) having similar salinities have lower δD and $\delta^{18}\text{O}$ values than water having higher salinities. Since DHO and H_2^{18}O have lower vapor pressure, they will evaporate at a lower rate than H_2^{16}O causing an enrichment of deuterium and oxygen-18 in an evaporation pool (see Swart et al. 1989 for further details on this process). Thus freshwater from evaporation pools may have low salinities but relatively high δD and $\delta^{18}\text{O}$ values, as shown in Fig. 2.

Discussion

With the scrub mangroves in the high salinity end of available water there is a stem water from plants in hardwood hammocks, even for a hammock with a water table having a salinity of 16%, and the transitional woodland have stem water with isotopic ratios similar to that of freshwater.

Fig. 4. Average δD values versus average $\delta^{18}\text{O}$. Values of plain stem water for different plant communities ($\delta D = -3.55 \pm 5.91$ ($\delta^{18}\text{O}$), $r^2 = 0.88$, $P < 0.01$). Number by each point represents the sites as designated in Fig. 3.

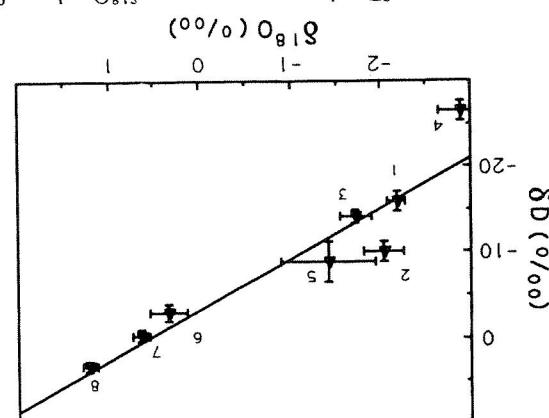


Table 1. Average predrawn water potentials, and isotopic composition of stem water (\pm SEM) from several plant species sampled at different sites in Sugar Loaf Key, having different plant communities.

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simple linear mixing model between ocean and freshwater. We hypothesize that there are several sites where salts, deposited inland by high tides, mix with rain water. The resulting ground water would have low $\delta^{18}\text{O}$ and δ^{D} values, indicating a mixture of freshwater, but high salinity similar to ocean water. Water potential measurements, together with measurements of isotopic composition of stem water indicate that the predawn water position of stem water for these communities is determined by different mixtures of ocean water and freshwater. However, the predawn water potential is often most negative at the conclusion of stem water for these communities. This position of stem water for most plant communities is typical of either freshwater or ocean water.

Our measurements indicate that the salinity of the coastal waters sampled here is not determined by a

Conclusions

The relationship between $\delta^{18}\text{O}$ values of plant water for the plant communities sampled here has a similar slope (5.9) as that observed between δD and $\delta^{18}\text{O}$ values of ground water (5.1). Average δD and $\delta^{18}\text{O}$ values of stem water for each community show a cluster-living towards the two extremes of isotopic composition of available water (Fig. 4). Plants from the MAN and RSM sites have stem water with a range of 10‰, while plants from the HL, HH, and TW sites cluster towards the freshwater end. This clustering may not only reflect the sharp interface between ocean water and freshwater, but may also reflect lack of sealing establishment where salinity changes at this interface occur rapidly enough to prevent accimation.

They may be caused by temporal variations in the isotopic ratios of the water available to the plant. Secondly, there could be a discrimination against heavy isotopes during plant water uptake under higher salinities, as has been previously observed (Sternberg and Smart 1987).

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